Effect of an Alternate Weed Host, Hairy Nightshade, *Solanum sarrachoides*, on the Biology of the Two Most Important Potato Leafroll Virus (Luteoviridae: Polerovirus) Vectors, *Myzus persicae* and *Macrosiphum euphorbiae* (Aphididae: Homoptera)

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ABSTRACT Hairy nightshade, *Solanum sarrachoides* (Sendtner), is a ubiquitous weed in potato agro-ecosystems and nonagricultural lands of southeastern Idaho and the Pacific Northwest. This weed increases the complexity of the Potato leafroll virus (PLRV) (Luteoviridae: *Polervirus*)–potato pathosystem by serving as aphid and virus reservoir. Previous field studies showed higher densities of green peach aphid, *Myzus persicae* (Sulzer), and potato aphid, *Macrosiphum euphorbiae* (Thomas), the two most important vectors of PLRV, on *S. sarrachoides* compared with potato plants in the same fields. Some of the *S. sarrachoides* plants sampled in these surveys tested positive for PLRV. Viral infections can alter the physiology of plant hosts and aphid performance on such plants. To understand better the potential effects of *S. sarrachoides* on the PLRV–potato–aphid pathosystem, the life histories of *M. persicae* and *M. euphorbiae* were compared on virus-free and PLRV-infected *S. sarrachoides* and potato. Individual nymphs of each aphid species were held in clip cages on plants from each treatment to monitor their development, survival, and reproductive output. Nymphal survival for both aphids across plant species was higher on *S. sarrachoides* than on potato, and, within plant species, it was higher on PLRV-infected plants than on noninfected plants. With a few exceptions, similar patterns occurred for fecundity, reproductive periods, adult longevity, and intrinsic rate of increase. The enhanced performance of aphids on *S. sarrachoides* and on PLRV-infected plants could alter the vector population dynamics and thus the PLRV-disease epidemiology in fields infested with this weed.

KEY WORDS alternate weed hosts, vector reservoir, viral inoculum source, insect vectors, vector performance

The presence of an alternate weed host potentially complicates classic viral pathosystems (host-virus-vector) (Irwin and Thresh 1990). In agro-ecosystems, weeds that are alternate hosts for an insect pest of the crop and a reservoir for a pathogen vectored by that insect can seriously complicate management (Duffus 1971, Norris and Kogan 2005). Hairy nightshade, *Solanum sarrachoides* (Sendtner), is a common solanaceous weed in the potato, *Solanum tuberosum* L., ecosystems of the Pacific Northwest. It is a host for Potato leafroll virus (PLRV) (Luteoviridae: Polerovirus) (Thomas 2002, Alvarez et al. 2003, Alvarez and Srinivasan 2005, Srinivasan et al. 2006) and several other potato viruses (R.S. and J.M.A., unpublished data), and is also a host for the two most important PLRV vectors, the green peach aphid, *Myzus persicae* (Sulzer), and the potato aphid, *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae).

Solanum sarrachoides supports substantially more aphids per plant than potato in agro-ecosystems of the Pacific Northwest (Alvarez and Srinivasan 2005). *Myzus persicae* preferentially settles on *S. sarrachoides* compared with potato (Srinivasan et al. 2006) and produces more nymphs on *S. sarrachoides* than on potato (Alvarez and Srinivasan 2005) and other hosts (Tamaki and Olsen 1979). Greater settling by and fecundity of *M. persicae* on *S. sarrachoides* potentially increase the build-up of its populations and subsequent dispersal to the potato crop. Additionally, the incidence of PLRV infection on *S. sarrachoides* was found to be typically higher than on potato plants in potato fields in the Pacific Northwest (Thomas 2002).

Viral infections can affect host nutritional quality by altering amino acids concentration (Markkula and Laurema 1964, Ajayi 1986) and soluble carbohydrates (Fereres et al. 1990). These and other changes influence aphid performance positively (Kennedy 1951, Macias and Mink 1969, Ajayi and Dewar 1983, Castle

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and Berger 1993, Eckel and Lampert 1996) and negatively (Blua and Perring 1992, Michels et al. 1994). Several vector life history studies conducted with host plants infected with either PLRV or barley yellow dwarf virus (BYDV) (Luteoviridae: Luteovirus) showed that aphids multiplied faster on virus-infected plants than on noninfected counterparts (Ponsen 1969, Fereres et al. 1989, Quiroz et al. 1991, Castle and Berger 1993, Jiménez-Martínez et al. 2004).

Seasonal dynamics of PLRV and aphids in the production landscape can also be affected by *S. sarrachoides.* Aphids colonize spring hosts including *S. sarrachoides* before dispersing to potato. Substantial vector population build-up in *S. sarrachoides*, especially if these plants have been infected by PLRV, could hasten disease spread in potato. Weeds like *S. sarrachoides* have also been documented to survive the winter on canals, ditches, and springs adjacent to heated buildings in the Pacific Northwest, and these weeds were found to support aphid populations that were likely to be viruliferous; hence, weed and aphid populations were found throughout the year (Wallis 1967a,b, Duffus 1971, Alvarez et al. 2003). Winter survival of secondary weed host plants presents a continuum of host availability for the virus and its vectors and could potentially affect the vector population build-up and PLRV disease spread. A clear understanding of aphid biology on *S. sarrachoides* and PLRV-infected hosts could help elucidate the role of *S. sarrachoides* in the complex PLRV pathosystem. The objective of this study was to investigate the life history parameters of two major PLRV vectors on *S. sarrachoides* with and without PLRV infection in comparison with potato. Detailed knowledge on vector life history parameters would help to substantiate the previous findings that *S. sarrachoides* positively affects *M. persicae*'s preference and performance (Alvarez and Srinivasan 2005, Srinivasan et al. 2006). *Macrosiphum euphorbiae* has been reported to be a less efficient PLRV vector than *M. persicae* (Tamada and Harrison 1981). However, *M. euphorbiae* has been observed in substantial numbers on *S. sarrachoides* in the Pacific Northwest potato fields, and such high vector populations, even with lower transmission ability, could significantly contribute to virus spread.

Materials and Methods

Host Plants and Aphids. Virus-free tissue culture–derived potato plantlets (cultivar Russet Burbank) were used to propagate potato plants for all experiments. They were obtained from the tissue culture facility at the University of Idaho, Moscow, ID, and repropagated using Murashige and Skoog (MS medium) basal salt medium with minimal organics (MS Sigma) at the Aberdeen Research & Extension (R & E) Center. Plantlets were potted in 10 by 10 by 15-cm plastic pots with a 2:2:1 potting mix (sand:peat:vermiculite) and 14:14:14 (N:P:K) encapsulated fertilizer (Osmocote; Scotts Miracle Gro, Marysville, OH) and maintained in the greenhouse at 19–27°C with a 16-h photoperiod. A colony of *M. persicae* clone 'OUR' initially collected by Dr. Guy W. Bishop from potato and maintained on Indian mustard, *Brassica juncea* L. Czern., for >25 yr, was obtained from Dr. Thomas M. Mowry, retired Entomologist, University of Idaho, Parma R & E Center. The colony has been maintained at the Aberdeen R & E Center since 2001 on Chinese cabbage, *Brassica pekinensis* (Ruprecht), in growth chambers at 21–26°C, 90% RH, and a 14-h photoperiod. Chinese cabbage is a host for *M. persicae* and a nonhost for potato viruses and was used to culture nonviruliferous *M. persicae.* Chinese cabbage seeds were obtained from a commercial facility and germinated and maintained in the greenhouse as described above.

Macrosiphum euphorbiae aphids were collected from potato fields in Aberdeen, ID. Field-collected aphids were initially maintained on rose, *Rosa*'BURway' plants, a nonhost for potato viruses, and newly laid nymphs (nonviruliferous nymphs) were transferred from rose to seed-raised *S. sarrachoides* plants. PLRV is not transmitted transovarially.

Solanum sarrachoides seeds were obtained from Dr. Pamela J.S. Hutchinson, University of Idaho, Aberdeen R & E Center. Seeds were sprouted in a petri dish lined with moist filter paper, sealed with laboratory film (Parafilm; American National Can, Greenwich, CT), and incubated in growth chambers at the abovementioned conditions. The sprouted seeds were planted in a greenhouse in plastic pots and maintained under the conditions stated above. Luteoviruses are not known to be seed transmitted.

Potato Leafroll Virus Inoculation and Titer Determination. Four-week-old potato plantlets were inoculated using viruliferous aphids that had fed for at least 96 h on PLRV-infected ground cherry, *Physalis floridana* (Rydberg), plants. Ten viruliferous *M. persicae* were allowed to feed on the virus-free potato plants for 96 h, after which they were removed with a no. 2 paint brush. After aphid removal, the potato plants were placed in chiffon cages (100 by 100 by 75 cm; one treatment per cage) in the greenhouse, which was immediately treated with the insecticide Dibrom 8 emulsive (Amvac Chemical, Los Angeles, CA) at a rate of 29.6 ml/283 m^3. The Dibrom treatment was repeated at weekly intervals until the initiation of the experiment to eliminate the possibility of aphid contamination. Inoculated potato plants were tested for the presence of PLRV using double antibody sandwich enzyme linked immunosorbent assay (DAS-ELISA; Anti PLRV IgG and Anti PLRV IgG conjugated with AP; BIOREBA AG, Nyon, Switzerland) (Clark and Adams 1977) 3 wk after inoculation with suitable positive and negative controls. Equal weight foliar samples (fresh weight, 1 g) from all treatments were used to compare the virus titer on the plants based on absorbance values at 405 nm; all the absorbance comparisons were made in a single microtiter plate. Additionally, plants from all treatments were carefully removed entirely from the pots, and their roots were washed free of debris and placed in a hot air oven at 70°C for 48 h. The dry weight of infected and noninfected roots and shoots of both species was analyzed using PROC ANOVA SAS 9.1 (SAS Institute, Cary,

NC). The treatment means were compared using Fisher least significant differences (LSDs).

Life History Studies. Six plants from each of the four treatments (PLRV infected and noninfected *S. sarrachoides* and potato) were used for this study. Experiments were initiated only after ELISA confirmation of viral infection status in treatment plants (3 wk after inoculation). Two adult *M. persicae* per plant were confined individually to leaf-cages (3 cm diameter and 2 cm tall) constructed from Bio-Quip vials (Rancho Dominguez, CA) with a chiffon bottom for a total of six replications per treatment (one replication = two leaf cages in one plant). The two leaf-cages were placed randomly in the top and or middle portion of the plant. The experiment was repeated with potato aphid *M. euphorbiae* and hence a total of 48 plants and 96 aphids were used for these experiments.

Adult aphids were placed on the ventral side of the treatment plant leaflets with a no. 2 camel-hair paint brush and confined individually in leaf-cages to lay nymphs. After 48 h, the adults were removed, and a single nymph was left in the cage. This single aphid in the cage was monitored until its death, and data on total nymphal period from birth to final molt alone were recorded. Mortality during the course of nymphal development on each treatment also was recorded. Nymphs turned adults were monitored daily, the number of nymphs produced by these adults also was recorded, and nymphs were removed from the cage daily. Adult longevity and prereproductive, reproductive, and postreproductive periods also were recorded. The intrinsic rate of increase (r_m) for each aphid was calculated as per the equation of Wyatt and White (1997): $r_m = c(\log N_d)/d$, where c is the constant 0.738 for aphids and mites, N_d is the number of nymphs produced in the reproductive period, and d is the preproductive time in days of the individual aphid. To study the effect of host plant species, and viral infection status, and their interaction on life history parameters of each aphid species, a three-way analysis of variance (ANOVA) was performed using PROC GLM SAS 9.1 (SAS Institute). The treatments were compared using paired orthogonal contrasts.

Results

Virus Titer and Plant Weight. Virus titer in PLRV-infected *S. sarrachoides* was almost four times lower than that in PLRV-infected potato ($F = 19.25$; df = 3,44; $P < 0.000$; Table 1). The mean dry weights of virus-infected plants of both species were significantly lower than the mean dry weights of noninfected plants ($F = 52.78$; df = 3,44; $P < 0.000$; Table 1).

Nymphal Survival. Because of experimental design constraints, nymphal survival was estimated as a numerical percentage, and no statistical analyses were performed. *M. persicae* and *M. euphorbiae* nymphal survival on PLRV-infected and noninfected *S. sarrachoides* was 83.34 and 100 and 100 and 100, respectively. *M. persicae* and *M. euphorbiae* nymphal survival on PLRV-infected and noninfected potato was 83.34 and 58.34 and 33.34 and 0%, respectively. Percent survival of *M. persicae* and *M. euphorbiae* nymphs was greater on *S. sarrachoides* (95.84%) than on potato (43.75%) (noninfected and PLRV-infected plants combined).

Table 1. PLRV titer in infected *S. sarrachoides* and potato plants and dry weights of plants

Source	Mean ± SE	*P*
Virus titer	OD	
Treatments		<0.0001
Potato-infected plants only	1.18 ± 0.24 a	
S. sarrachoides-infected plants only	0.30 ± 0.08 b	
Plant dry weight	(g)	
Treatments		<0.0001
Potato non-infected plants	36.00 ± 3.60 a	
Potato-infected plants	12.79 ± 1.84 b	
S. sarrachoides noninfected plants	31.20 ± 2.78 a	
S. sarrachoides infected plants	6.54 ± 1.24 b	

Treatments with the same letters are not significantly different from each other based on a LSD test ($\alpha = 0.05$).

OD, optical density or the absorbance values measured using a Biotek Photometer set at 405 nm.

Total Life Cycle. Both host infection status and host species affected the aphid survival, and the effects varied with aphid species (Fig. 1a; Table 2). Three-way and two-way interactions were noticed among and between all the involved factors. *M. persicae* survived longer on *S. sarrachoides* than on potato, irrespective of PLRV infection ($F = 11.78$; df = 1,38; $P = 0.001$). The same effect was observed in *M. euphorbiae* ($F = 78.89$; df = 1,38; $P = <0.000$). Total life span of *M. persicae* on PLRV-infected *S. sarrachoides* was longer than on noninfected *S. sarrachoides* ($F = 12.82$; df = 1,38; P 0.001). It was also longer on PLRV-infected than on noninfected potato. However, the difference was not significant ($F = 1.68$; df = 1,38; $P = 0.204$). Total life span of *M. euphorbiae* was longer on PLRV-infected *S. sarrachoides* ($F = 23.78$; df = 1,38; $P < 0.000$) and PLRV-infected potato ($F = 110.86$; df = 1,38; $P < 0.000$) compared with the noninfected plants of each host species.

Nymphal Longevity. Nymphal longevity varied with PLRV infection, and the effects varied with aphid species. Nymphal longevity was not affected by host species. Interaction was noticed among all three factors. Interactions were also noticed between host infection status and aphid species and between host species and aphid species (Fig. 1b; Table 2). *M. persicae* nymphal period was longer on PLRV-infected *S. sarrachoides* than on noninfected *S. sarrachoides* ($F = 8.59$; df = 1,38; $P = 0.006$). This did not occur on potato ($F = 2.85$; df = 1,38; $P = 0.101$). *M. euphorbiae* nymphs lived longer on PLRV-infected potato than on noninfected potato ($F = 23.08$; df = 1,39; $P = 0.000$). Although *M. euphorbiae* nymphs also lived longer on PLRV-infected *S. sarrachoides* than on noninfected *S. sarrachoides*, the difference was not significant ($F = 0.00$; df = 1,39; $P = 1.000$). In fact, contrasts showed no differences in nymphal longevity between host species irrespective of PLRV infection for *M. persicae* ($F = 3.53$; df = 1,38; $P = 0.070$) and *M. euphorbiae* ($F = 0.65$; df = 1,39; $P = 0.427$).

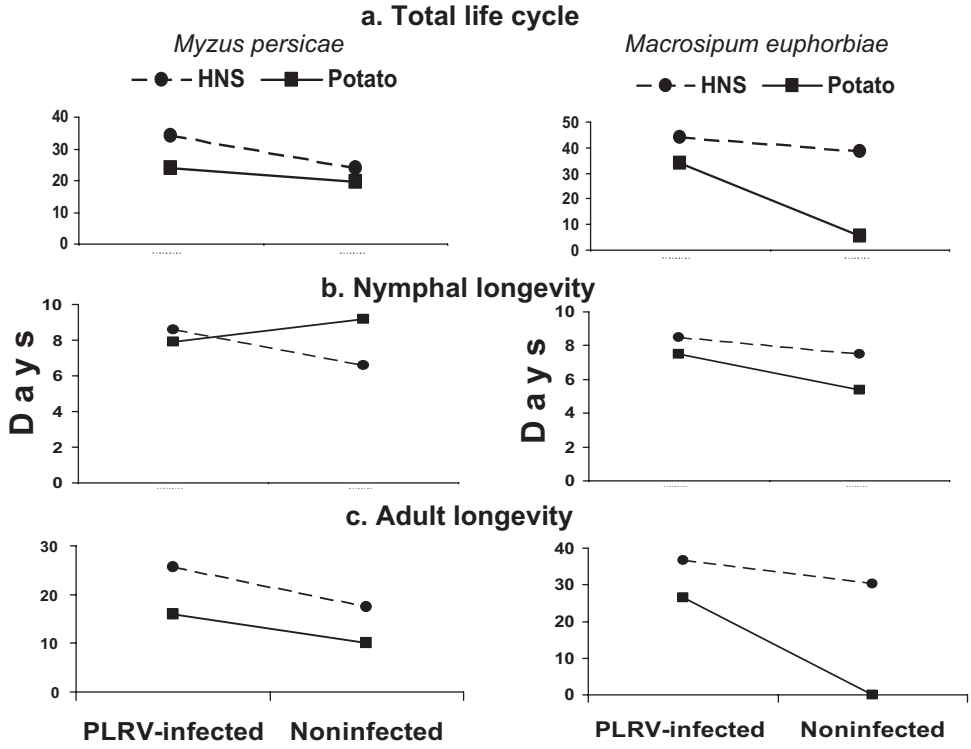

Fig. 1. The effect of *S. sarrachoides* and potato with and without PLRV infection on the (a) total lyfe cycle, (b) nymphal longevity, and (c) adult longevity of *M. persicae* and *M. euphorbiae*. Lines represent mean parameter values in days.

Adult Longevity. Adult longevity was affected by host species and host infection status and varied with aphid species (Fig. 1c; Table 2). Three-way and two-way interactions were noticed among and between all the involved factors. Adults of *M. persicae* ($F = 13.46$; df = 1,38; $P = 0.000$) and *M. euphorbiae* ($F = 94.17$; df = 1,39; $P < 0.000$) lived longer on *S. sarrachoides* than on potato (Fig. 1c; Table 2). Adult longevity of *M. persicae* ($F = 7.99$; df = 1,38; $P = 0.008$) and *M. euphorbiae* ($F = 29.59$; df = 1,39; $P < 0.000$) was longer on PLRV-infected *S. sarrachoides* than on noninfected *S. sarrachoides*. *M. persicae* adult longevity did not differ between PLRV-infected and noninfected potato ($F = 2.51$; df = 1,38; $P = 0.123$). However, it was different in *M. euphorbiae* ($F = 110.85$; df = 1,39; $P < 0.000$).

Prereproductive Period. Prereproductive period was affected by host infection status and host species, and the effects varied with aphid species; Interaction was noticed among all the three factors (Fig. 2a; Table 2). Two-way interactions were noticed between host infection status and aphid type and also between host species and aphid species. Contrasts showed that the *M. persicae* prereproductive period was not different between PLRV-infected and noninfected *S. sarrachoides* ($F = 0.80$; df = 1,38; $P = 0.378$) and potato ($F = 0.00$; df = 1,38; $P = 0.967$). However, the prereproductive period was longer on *S. sarrachoides* than on potato ($F = 4.66$; df = 1,38; $P = 0.038$). *M. euphorbiae* prereproductive period was longer on PLRV-infected *S. sarrachoides* ($F = 17.32$; df = 1,39; $P = 0.000$) and potato ($F = 33.09$; df = 1,39; $P < 0.000$) than on their noninfected counterparts. Like in the case of *M. persicae*, *M. euphorbiae*'s prereproductive period was longer on *S. sarrachoides* than on potato, irrespective of PLRV infection ($F = 25.66$; df = 1,39; $P < 0.000$).

Reproductive Period. The reproductive period of aphids was affected by both host infection status and host species (Fig. 2b; Table 2); interaction was noticed between host infection status and aphid species. The reproductive period of *M. persicae* was longer on PLRV-infected *S. sarrachoides* ($F = 5.30$; df = 1,38; $P = 0.028$) and potato than on noninfected plants. However, the difference was not significant on potato ($F = 1.81$; df = 1,38; $P = 0.188$). *M. euphorbiae* reproductive period was longer on PLRV-infected *S. sarrachoides* than on noninfected *S. sarrachoides* ($F = 36.60$; df = 1,39; $P < 0.000$). *M. euphorbiae* did not survive as adults on noninfected potato ($F = 46.20$; df = 1,39; $P < 0.000$). Irrespective of PLRV infection, reproductive periods of both *M. persicae* ($F = 11.45$; df = 1,38; $P = 0.002$) and *M. euphorbiae* ($F = 90.33$; df = 1,39; $P < 0.000$) were longer on *S. sarrachoides* than on potato.

Postreproductive Period. Postreproductive survival in both *M. persicae* and *M. euphorbiae* was affected by host infection status. There was a significant three-way interaction among involved factors (Fig. 2c; Table 2). Significant two-way interactions were also noticed between host infection status and host species and between host infection status and aphid species. The

Table 2. Three-way ANOVAs for various life history parameters of both *M. persicae* and *M. euphorbiae* and their interaction with *S. sarrachoides* and potato, with or without PLRV infection

Factors	*F*	Type III SS	*P* > *F*
Total life cycle			
Infection	99.24	3,643.12	<0.000
Plant	70.48	2,587.55	<0.000
Infection × plant	9.03	331.46	0.003
Aphid	12.63	463.59	0.000
Infection × aphid	24.68	902.51	<0.000
Plant × aphid	10.67	391.62	0.001
Infection × plant × aphid	24.41	896.27	<0.000
Nymphal longevity			
Infection	8.33	14.23	0.005
Plant	0.44	0.75	0.508
Infection × plant	0.04	0.05	0.851
Aphid	7.90	13.49	0.006
Infection × aphid	4.06	6.94	0.047
Plant × aphid	5.70	9.73	0.019
Infection × plant × aphid	25.90	44.25	<0.000
Adult longevity			
Infection	85.38	3,201.91	<0.000
Plant	71.38	2,676.65	<0.000
Infection × plant	9.08	340.44	0.003
Aphid	16.94	635.30	0.000
Infection × aphid	20.03	751.14	<0.000
Plant × aphid	7.41	277.88	0.008
Infection × plant × aphid	14.46	542.20	0.000
Prereproductive period			
Infection	32.54	16.34	<0.000
Plant	29.28	14.70	<0.000
Infection × plant	2.25	1.13	0.013
Aphid	15.18	7.62	0.000
Infection × aphid	28.01	14.06	<0.000
Plant × aphid	9.87	4.95	0.002
Infection × plant × aphid	4.68	2.35	0.033
Reproductive period			
Infection	45.03	1,339.04	<0.000
Plant	58.04	1,726.06	<0.000
Infection × plant	0.80	23.68	0.375
Aphid	0.05	1.59	0.817
Infection × aphid	4.49	133.42	0.037
Plant × aphid	2.14	63.73	0.147
Infection × plant × aphid	2.31	68.81	0.132
Postreproductive period			
Infection	23.72	254.39	<0.000
Plant	3.77	40.39	0.056
Infection × plant	14.62	156.77	0.000
Aphid	52.40	562.08	<0.000
Infection × aphid	13.66	146.53	0.000
Plant × aphid	3.89	41.72	0.052
Infection × plant × aphid	16.88	181.06	0.000
Total fecundity			
Infection	22.80	3,001.59	<0.000
Plant	48.40	6,350.52	<0.000
Infection × plant	6.11	802.29	0.015
Aphid	1.33	174.86	0.252
Infection × aphid	4.02	527.67	0.048
Plant × aphid	6.99	916.83	0.010
Infection × plant × aphid	0.41	54.31	0.522
Daily fecundity			
Infection	1.90	1.266	0.172
Plant	15.41	10.29	0.000
Infection × plant	23.69	15.82	<0.000
Aphid	0.12	0.07	0.731
Infection × aphid	1.63	1.08	0.206
Plant × aphid	10.14	6.77	0.002
Infection × plant × aphid	0.48	0.31	0.494
Intrinsic rate of increase			
Infection	434.74	13.75	<0.000
Plant	618.79	19.57	<0.000
Infection × plant	306.59	9.69	<0.000
Aphid	2,900.35	91.73	<0.000
Infection × aphid	408.52	12.92	<0.000
Plant × aphid	519.71	16.43	<0.000
Infection × plant × aphid	210.94	6.67	<0.000

Three-way ANOVA was performed using Proc GLM in SAS to estimate the effect of factors whether alone or in interaction on life history parameters of *M. persicae* and *M. euphorbiae*. df = 1,77. $P < 0.05$ indicates that the factors either alone or in interaction have a significant effect.

M. euphorbiae postreproductive period was similar on PLRV-infected and noninfected *S. sarrachoides* ($F = 0.11$, df = 1, 39, $P = 0.745$) and longer on PLRV-infected potato than on noninfected potato ($F = 30.83$; df = 1,39; $P < 0.000$). Irrespective of PLRV infection, the postreproductive period was longer on *S. sarrachoides* than on potato ($F = 4.92$; df = 1,39; $P < 0.034$). However, the postreproductive period for *M. persicae* was not different between PLRV-infected and noninfected *S. sarrachoides* ($F = 1.87$; df = 1,38; $P = 0.181$) and potato ($F = 0.55$; df = 1,38; $P = 0.465$).

Total Lifetime and Daily Fecundity. Lifetime fecundity in both *M. persicae* and *M. euphorbiae* was affected by host species and host infection status. Two-way interactions were noticed between all the factors involved (Fig. 3a; Table 2). *M. persicae* lifetime fecundity was higher on *S. sarrachoides* than on potato, irrespective of plant infection status ($F = 6.25$; df = 1,38; $P = 0.018$). Total lifetime fecundity did not differ between infected and noninfected *S. sarrachoides* ($F = 0.00$; df = 1,38; $P = 0.970$). Total lifetime fecundity was higher on potato-infected plants (mean ± SE: 24.1 ± 5.01) than on noninfected potato plants (7.85 ± 1.68; $F = 4.00$; df = 1,38; $P = 0.054$). *M. euphorbiae* lifetime fecundity was higher on *S. sarrachoides* than on potato, irrespective of infection status ($F = 133.56$; df = 1,39; $P < 0.000$). Fecundity was greater on PLRV-infected *S. sarrachoides* than on noninfected *S. sarrachoides* ($F = 27.88$; df = 1,39; $P < 0.000$). *M. euphorbiae* did not survive as adults on noninfected potato plants, and consequently, the fecundity was higher on PLRV-infected plants ($F = 31.12$; df = 1,39; $P < 0.000$).

Daily fecundity of both *M. persicae* and *M. euphorbiae* was only affected by host species (Fig. 3b; Table 2). Irrespective of infection status, daily fecundity of *M. persicae* was the same in both host species ($F = 0.69$; df = 1,38; $P = 0.414$) but was greater on *S. sarrachoides* for *M. euphorbiae* ($F = 15.85$; df = 1,39; $P = 0.000$). Within each plant species, *M. persicae* daily fecundity was higher on noninfected *S. sarrachoides* than PLRV-infected *S. sarrachoides* ($F = 6.37$; df = 1,38; $P = 0.017$) and on PLRV-infected potato than noninfected potato ($F = 5.38$; df = 1,38; $P = 0.027$). In the case of *M. euphorbiae*, daily fecundity was similar between infected and noninfected *S. sarrachoides* ($F = 2.25$; df = 1,39; $P = 0.143$). However, it was higher in PLRV-infected potato than on noninfected potato ($F = 7.96$; df = 1,39; $P = 0.000$).

Intrinsic Rate of Increase. Intrinsic rate of increase was affected by all the three factors: host infection status, host species, and aphid species (Fig. 3c; Table 2). This is explained by three- and two-way interactions with all the factors involved (Table 2). Irrespective of plant infection status, *M. persicae* intrinsic rate of increase was greater on *S. sarrachoides* than on potato ($F = 6.45$; df = 1,38; $P = 0.015$). The same was observed with *M. euphorbiae* ($F = 86.86$; df = 1,39; $P < 0.000$). In *M. persicae*, the intrinsic rate of increase was not different between infected and noninfected *S. sarrachoides* ($F = 3.35$; df = 1,38; $P = 0.077$) but was higher on PLRV-infected potato than on noninfected potato ($F = 6.63$; df = 1,38; $P = 0.015$). *M. euphorbiae*

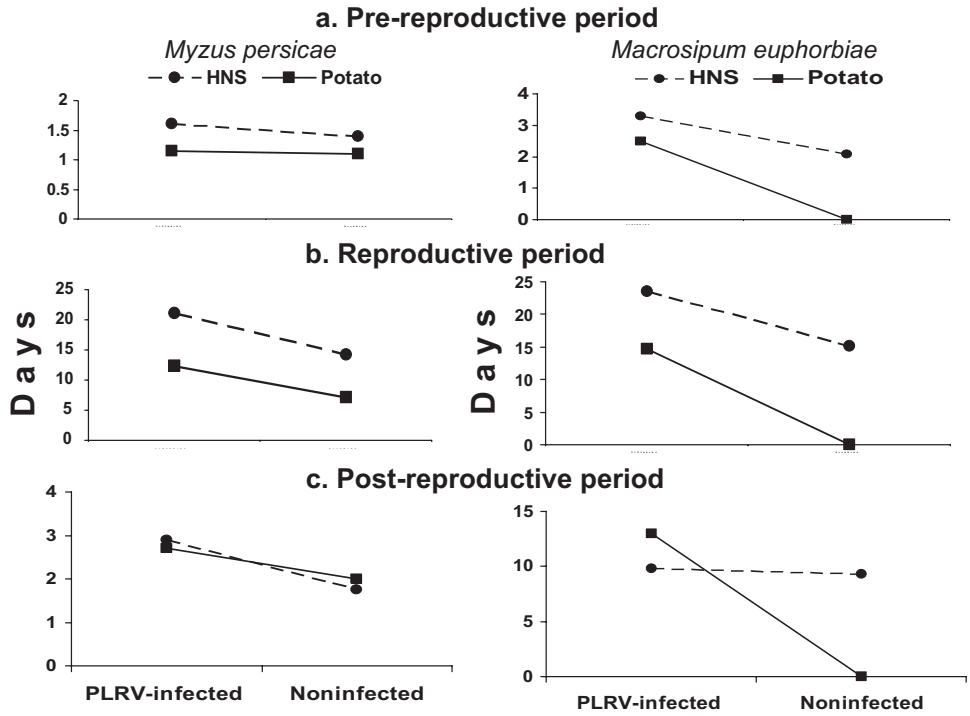

Fig. 2. The effect of *S. sarrachoides* and potato with and without PLRV infection on the (a) prereproductive period, (b) reproductive period, and (c) postreproductive period of *M. persicae* and *M. euphorbiae*. Lines represent mean parameter values in days.

intrinsic rate of increase was not different between PLRV-infected *S. sarrachoides* ($F = 0.58$; df = 1,39; $P = 0.452$) and noninfected *S. sarrachoides.* However, it was higher on PLRV-infected potato ($F = 32.27$; df = 1,39; $P < 0.000$) compared with noninfected potato.

Discussion

Performance of aphids varies with plant hosts. In our study, performance of *M. persicae* and *M. euphorbiae* measured in terms of various life history parameters such as longevity, reproductive periods, total lifetime fecundity, and intrinsic rate of increase indicated that *S. sarrachoides* is a superior host for aphid multiplication than potato. Previous research also showed that fecundity of *M. persicae* during a 48-h period was 23.9% greater on *S. sarrachoides* than on potato (Alvarez and Srinivasan 2005). Our results indicate that host plants belonging to the same genus could have contrasting effects on the biology of highly polyphagous aphids like *M. persicae* and *M. euphorbiae.* For instance *M. euphorbiae* nymphs survived only on *S. sarrachoides* but not on potato plants. These results reiterate the fact that host plant–vector relationships are very intricate and vary on case by case basis.

Host plant–vector interactions can further be altered by viral infections. Viral infections may induce host symptom expression and can affect the nutritional profile. These changes are known to influence the performance of aphids both positively and negatively (Kennedy 1951, Selman et al. 1961, Ajayi and Dewar 1983, Blua and Perring 1992, Castle and Berger 1993, Michels et al. 1994, Eckel and Lampert 1996, Kift et al. 1996). In our tests, PLRV-infected plants of both species exhibited typical PLRV disease symptoms including severe stunting. This stunting resulted in lower dry weights of virus-infected plants. PLRV-infected *S. sarrachoides* plants had lower virus titers than infected potato plants as previously reported (Alvarez and Srinivasan 2005).

Alterations in aphid performance caused by viral infection are evidenced by changes in life history parameters of both *M. persicae* and *M. euphorbiae.* Nymphal survival of *M. euphorbiae* increased by 33% on PLRV-infected potato plants compared with noninfected potato plants. Observations indicated that nymphs and adults of *M. persicae* lived longer on PLRV-infected *S. sarrachoides* than on noninfected *S. sarrachoides.* However, this difference was not observed in potato. Adults of *M. euphorbiae* lived longer on PLRV-infected *S. sarrachoides* and potato than on the same noninfected plants. The fecundity and intrinsic rate of increase of *M. euphorbiae* were greater on PLRV-infected *S. sarrachoides* and potato than on noninfected host plants. The fecundity and intrinsic rate of increase of *M. persicae* were also greater on PLRV-infected potato than on noninfected plants. These results are consistent with Ponsen (1969) and Castle and Berger (1993), who also reported higher *M. persicae* intrinsic rates of increase on PLRV-infected

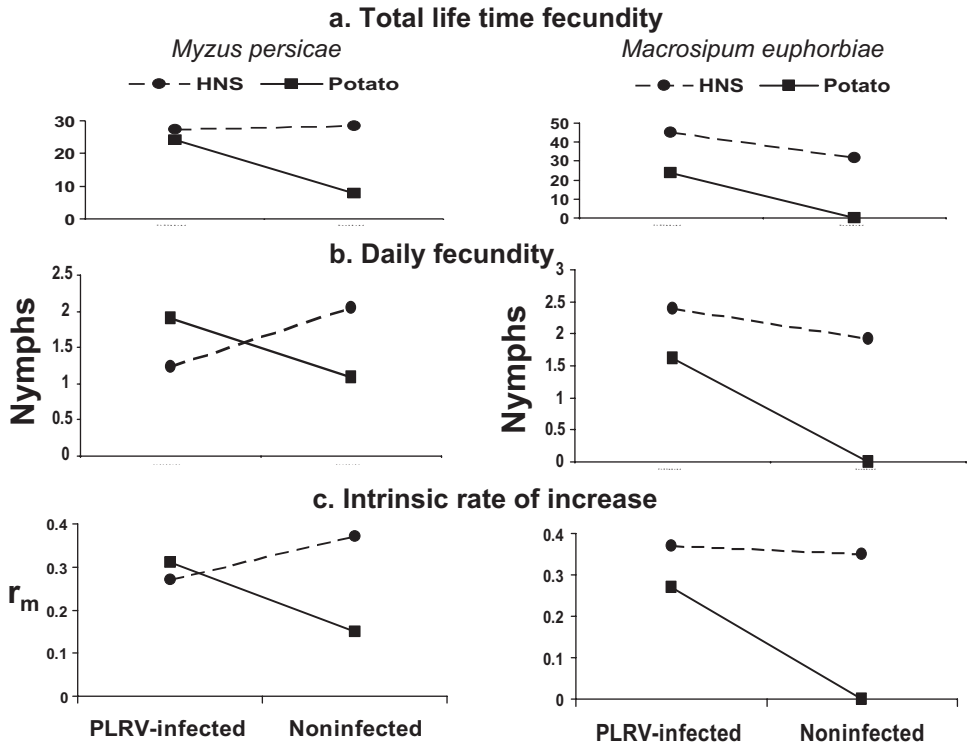

Fig. 3. The effect of *S.sarrachoides* and potato with and without PLRV infection on the (a) total life time fecundity, (b) daily fecundity, and (c) intrinsic rate of increase of *M. persicae* and *M. euphorbiae*. Lines represent mean parameter values as nymphs.

potato and *P. floridana* plants than on noninfected plants. Thus, PLRV infection in host plants could influence aphids positively. The exact physiological basis of the responses observed in these studies are unknown but could be affected by changes in nutritional quality, concentrations of deterrents, feeding stimulants, or toxicants in phloem related to infection status (Irwin and Thresh 1990, Power and Gray 1995, Guntner et al. 1997, Karley et al. 2002).

Positive effects of Luteoviruses on vector performance, although not universal, seem to be a very common occurrence (Ponsen 1969, Fereres et al. 1989, Quiroz et al. 1991, Castle and Berger 1993, Power and Gray 1995, Jiménez-Martínez et al. 2004). The interactions between Luteoviruses such as PLRV and BYDV and their vectors are postulated to be mutualistic and tightly coevolved, leading to increased fitness of the vector and propagation of the virus (Castle and Berger 1993, Power and Gray 1995).

Enhanced aphid performance on PLRV-infected *S. sarrachoides* coupled with increased PLRV transmission from *S. sarrachoides* as shown in a previous study (Alvarez and Srinivasan 2005) could also lead to increased vector fitness and PLRV propagation in the potato PLRV pathosystem.

Solanum sarrachoides is an annual weed assumed to not survive the winter in the Pacific Northwest, and PLRV is not seed-transmitted. Therefore, *S. sarrachoides* has not been considered an important PLRV inoculum source in the region, nor have annual weeds in general been considered important inoculum sources for viruses affecting the potato crop (Thomas 1983). However, in the Pacific Northwest, winter survival of *M. persicae* on weeds has been documented (Wallis 1967a,b, Duffus 1971, Alvarez et al. 2003). Even if overwintering *S. sarrachoides* is as rare as to be an inconsequential source of viral inoculum, preferred alightment and colonization of aphids on *S. sarrachoides* early in the spring could enhance the build-up of aphid populations in the field and subsequent dispersal to the crop. Other annual weeds have been known to act as bridges for virus and vectors before the emergence of crops. For example, Groves et al. (2002) described such an effect in the tomato spotted wilt virus (Bunyaviridae: Tospovirus) system. They reported the overwintering of tobacco thrips, *Frankliniella fusca* (Hinds), on winter annual weeds infected with tomato spotted wilt virus and quoted that these weeds serve as a bridge for vectors and virus before the planting of susceptible crops.

Myzus persicae and *M. euphorbiae*, the two most important aphid vectors of PLRV in the Pacific Northwest, are capable of transmitting an array of viruses besides PLRV. This study indicates *S. sarrachoides* enhances the fitness of these vectors and could aggravate the spread of PLRV and potentially other viruses in the Pacific Northwest potato ecosystems. Other *Solanum* weeds such as *S. lycocarpum* (St. Hill),

S. erainthum (Dunn.), *S. paniculatum* L., and *Datura stramonium* L. have also been reported to increase PLRV infection in potato fields planted with high-grade seed material (Souza-Diás et al. 1993, Hanafi et al. 1995). Hence, populations of *S. sarrachoides* should be kept at a minimum. Management of *S. sarrachoides* is difficult because it is closely related to potato and is also a prolific seed producer. Stringent management options should be advocated to combat this weed and, some management options for this weed are suggested by Alvarez and Hutchinson (2005).

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